

LINKAGES BETWEEN MICROBIAL AND HYDROLOGIC PROCESSES IN ARID AND SEMIARID WATERSHEDS

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Abstract. Microbial activity in semiarid and arid environments is closely related to the timing, intensity, and amount of precipitation. The characteristics of the soil surface, especially the influence of biological soil crusts, can determine the amount, location, and timing of water infiltration into desert soils, which, in turn, determines the type and size of microbial response. Nutrients resulting from this pulse then create a positive feedback as increases in microbial and plant biomass enhance future resource capture or, alternatively, may be lost to the atmosphere, deeper soils, or downslope patches. When rainfall intensity overwhelms the water infiltration capacity of the plant interspace or the plant patch, overland water flow links otherwise separated patches at many different scales via the transport of nutrients in water, soil, and organic matter. For example, material carried from the plant interspace is often deposited under an adjacent plant. Alternatively, material from both of these patches may be carried to rills that feed ephemeral channels, thence to seasonally intermittent and, finally, perennial streams. These inputs can either be retained by the stream–riparian ecosystem or be exported in surface flow. However, in larger perennial streams, the fate of these material inputs is confounded by the impact of storm-driven flows on the extant aquatic biota, as flash floods can also represent succession-initiating disturbances to the stream–riparian ecosystem on a wide range of time scales. In contrast to uplands where precipitation initiates the microbial response, nutrient transfers can support a flush of plant uptake and microbial processing, triggered by high nutrient concentrations and changed nutrient form (e.g., nitrate or ammonium). The nature and strength of the linkages between the different ecosystem components define the structure and function of arid ecosystems. Losses of materials are natural processes, but it is problematic when “conserving” systems become “leaky” via anthropogenic disturbance and losses exceed gains.

Key words: activity pulse; biological soil crusts; desert; infiltration; nutrient cycling; precipitation.

INTRODUCTION

There is substantial evidence that human domination of Earth's ecosystems has had and will increasingly have profound effects, both direct and indirect, on the hydrologic cycle, with deserts particularly sensitive to changes in availability and delivery (e.g., precipitation amount and regime) of water. Furthermore, desert regions exhibit stark contrasts between adjacent terrestrial and aquatic ecosystems due to water availability, and it is here that study of linkages between such distinctive landscape components may be most profitable. An integrated understanding of water-driven microbial and biogeochemical processes in poorly understood desert landscapes is an important scientific challenge.

Events in upland patches influence what is delivered to recipient aquatic patches, and the structure and function of aquatic patches in turn influence groundwaters, reservoirs, and larger rivers.

Resource availability is driven by water in arid and semiarid ecosystems (Noy-Meir 1973). The amount, timing, and intensity of precipitation are highly variable and create pulses of activity in soils, plants, and animals that also vary on both spatial and temporal scales (Sala and Lauenroth 1982). Low nutrient availability in desert soils restrains primary productivity (Penning de Vries and Djiteye 1982). This nutrient limitation is partially due to the limited time soils are moist and, thus, the time microbes are active. However, even small amounts of precipitation can activate soil surface microbes and microbial processes (e.g., microbial processing of organic matter as a primary source of plant-available nutrients), unlike vascular plants that may require events of a minimum size or seasonal timing (Schwinning et al. 2002). Most microbial activity rates

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are also temperature dependent and some are light and substrate dependent, so daily and seasonal timing of precipitation can also determine activity rates. In addition, length of time between events can influence microbial responses in two contrasting ways. First, long dry periods can result in high microbial mortality, due to desiccation and radiation damage, leaving fewer microbes to respond to the pulse event (Castenholz and Garcia-Pichel 2000). Microbial mortality also results in a flush of nutrients for microbial uptake once water is available. Second, atmospherically deposited materials (e.g., N, dust) can build up in both upland and riparian soils during dry periods and may alleviate resource limitation to microbes when precipitation occurs (Verrecchia et al. 1995). Wetter areas of arid regions such as riparian zones are sustained by precipitation that recharges ground water, but microbial processes in these areas respond to episodic events as well; indeed, it is runoff that creates the pulsed connection between upland and stream components of arid landscapes.

Overland flow is regulated by soil infiltration capacity and rainfall intensity, and is a primary pathway in the transfer of soil, microbes, seeds, and plant litter over large distances, connecting otherwise isolated systems. This material transfer can occur at all scales, including plant interspace to downslope plants (1-m scale), hillslopes to intermittent drainages (100-m scale), and intermittent drainages to larger perennial streams (1-km scale). Given that water availability is a key driver of microbial processes in arid ecosystems, the amount, timing and intensity of precipitation events interacts with landscape structure, influencing whether materials are absorbed by receiving patches or transferred downslope (e.g., interspace to plant patch, hillslope to drainage network) and thus, where and when pulses of microbial activity occur in the landscape. Anthropogenic disturbance can profoundly affect these linkages, changing systems that retain nutrients, soil, and water ("conserving") into ones that lose resources ("leaky").

Dryland ecosystems exist across a gradient of mean annual precipitation from very arid to semiarid. Although our discussion draws on research in North American deserts, we emphasize that the processes we describe are "average" conditions for a "typical" year. Just as there is a gradient in mean conditions among ecosystems arrayed in space, any given location exhibits variation in time that is in many ways parallel to the spatial dimension. For instance, a Sonoran Desert watershed under long-term study shows pronounced interannual variability in rainfall, upland processes, and streamflow that translates to great variation in nitrogen (N) delivery to the stream (Grimm and Fisher 1992). Lessons from wetter portions of climatic gradients may cautiously be applied to wetter years at a single location. During wet years or at wetter sites, for example, we expect higher soil moisture and understo-

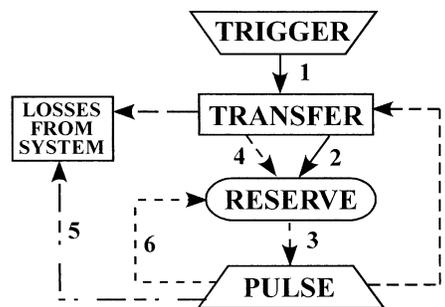


FIG. 1. A conceptual framework representing sequences of landscape ecological and hydrological processes and feedback loops. Examples of processes are (1) rainstorm; (2) infiltration, capture, and retention or storage; (3) plant germination, nutrient mineralization, and uptake processes; (4) soil loss, runoff into streams, rill flow, and erosion; (5) herbivory, leaching, fire, harvesting, and deep drainage; (6) biomass increase, nutrient availability, and organic matter cycling; and (7) physical obstruction/absorption processes.

ry growth, as well as greater infiltration, deep seepage, and patch linkage via subsurface flow in the uplands, and greater connectivity between streams and riparian zones.

In this paper, we explore the effect of precipitation pulses on microbial communities and microbially mediated nutrient cycles at these three different scales in hot and cool deserts, following the path of water beginning with the upland system and ending with stream networks. The trigger-transfer-reserve-pulse (TTRP) framework (Ludwig and Tongway 1997) is used to generalize our discussion. The TTRP framework contains both spatial and temporal elements and is focused on process (Fig. 1). For this paper, the trigger is rainfall. This trigger results in the vertical or horizontal transfer of materials (e.g., water, nutrients, soil). Resources may be absorbed into the receiving patch (the reserve) or leave the system. Absorbed resources result in a resource pulse (e.g., microbial activity) that can either be retained or lost from the patch. This framework recognizes landscape components are connected via the transfer of materials and emphasizes feedback processes that regulate and maintain landscape function.

UPLANDS: PATCH TO THE HILLSLOPE SCALE

Reserves: plant interspaces

Desert landscapes, plant islands, and hillslopes comprise a diversity of patches formed by plants and plant interspaces (Schlesinger et al. 1990, Puigdefabregas et al. 1999). At larger spatial scales, these patches are arrayed on hillslopes that often occur along topographic gradients from ridge tops to valley bottoms.

Plant interspace patch.—Soils between the widely spaced vascular plants in deserts are generally covered by a community of cyanobacteria, lichens, and mosses collectively called biological soil crust (BSC). This community can cover up to 70% or more of desert ground surfaces, and thus mediate most gas, nutrient,

Reserve = Soil Crust Community

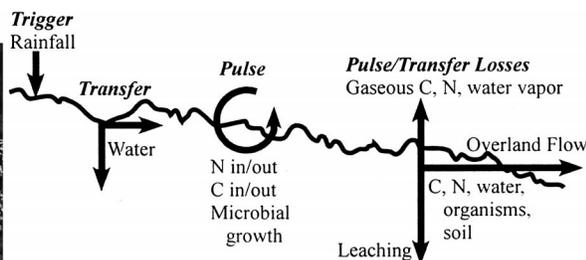
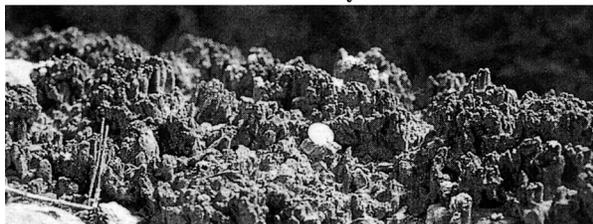


FIG. 2. TTRP (trigger–transfer–reserve–pulse) model applied to the plant interspace. The trigger is precipitation, and the reserve is the soil biotic community. Pulses discussed here include N and C dynamics. Transfer and losses include water, C, N, organisms, and soil.

and water inputs to, and losses from, desert soils. In cool deserts (e.g., Colorado Plateau), BSCs are dominated by a rich lichen–moss flora, whereas hot desert (e.g., Sonoran) BSCs are dominated by cyanobacteria. In all deserts, cyanobacteria dominate disturbed surfaces (Belnap and Eldridge 2003). These interspace areas can also support a significant cover of annual plants in wet years.

Plant island patch.—Plant-island patches vary in size and composition, depending on vegetation structure, which is driven primarily by soil type and rainfall. In hot deserts, soils under plants typically have higher organic matter, nutrient content (Schlesinger et al. 1996, Kieft et al. 1998), and microbial biomass (Gallardo and Schlesinger 1992) than interspace soils. Materials become concentrated in plant patches through the accumulation of plant litter and/or physical redistribution (Hook et al. 1991, Ludwig et al. 2005), as well as nitrogen fixation associated with leguminous plants (Virginia and Jarrell 1983). In cool deserts, organic matter is similarly higher under plants than interspaces. However, depending on the type of the nutrient, plant, or interspace being considered, nutrients are not always more concentrated under the shrubs, most likely due to high biomass of BSCs (Charley and West 1975, Doescher et al. 1984, Bolton et al. 1993).

Hillslopes.—At a larger scale, plant islands and interspaces are arrayed on hillslopes that contain varied geomorphic surfaces, including coalesced alluvial fans and highly dissected inset soils forming discontinuous channels. At the scale of a hillslope, more organic matter, nutrients, and microbial biomass accumulate in valley bottoms relative to hilltops (Gallardo and Schlesinger 1992, Burke et al. 1999). Thus convergent areas where resource availability is concentrated on the hillslope (e.g., topographic depressions) may be “primed” to elicit greater microbial responses to moisture pulses than divergent areas where resource availability is low due to increased erosion.

Transfers: horizontal and vertical movement of water, sediments, and nutrients

Ultimately, it is the relationship between the intensity of rainfall and infiltration on the individual patch

(interspace or plant island) that determines whether materials are absorbed by the receiving patch or transferred downslope. Variables that influence this relationship include topographic position, aspect, slope, hydraulic conductivity, and the presence, structure, and arrangement of vegetation and ground surface cover (Tongway and Ludwig 1997, Puigdefabregas et al. 1999).

The biomass and external morphology of BSCs dramatically influence how water moves across and into soil (Fig. 2). In hot deserts where soils do not freeze, BSCs smooth soil surfaces and generally increase runoff to downslope plant patches, regardless of precipitation event size. Where soils freeze, BSCs create mounds that greatly roughen the soil surface, preventing runoff from the interspace patch except during extreme monsoonal events (Belnap 2003). BSC mounds are oriented ENE to maximize photosynthetic efficiency and can thus differentially affect water flow velocity and direction, depending on the relationship between slope, aspect, and their orientation. When annual vascular plants occur in plant interspaces during wet years, they also slow the transfer of sediment or water from the plant interspace to the plant canopy. Under shrubs, higher concentrations of fine sediment, organic matter, and faunal burrowing activity often result in higher infiltration rates, and thus greater water and nutrient absorption, than interspace soils (Abrahams and Parsons 1991). However, under-plant materials may be hydrophobic, reducing infiltration compared to adjacent biologically crusted interspaces (D. Chandler and J. Belnap, unpublished data).

Connectivity among plant islands and interspace patches and the spatial patterning of soil water and nutrients on hillslopes is influenced by the characteristics of storms, interspaces, plant community structure, and topography (Puigdefabregas et al. 1999, Belnap 2003). When rainfall rates exceed interspace or plant-island infiltration rates, the resultant overland flow horizontally redistributes water, sediment, and nutrients. Losses from interspaces are influenced by BSC composition, where sediment, water, and associated C and N fluxes are higher from cyanobacterial BSCs relative to lichen BSCs (Barger 2003). Runoff nutrient

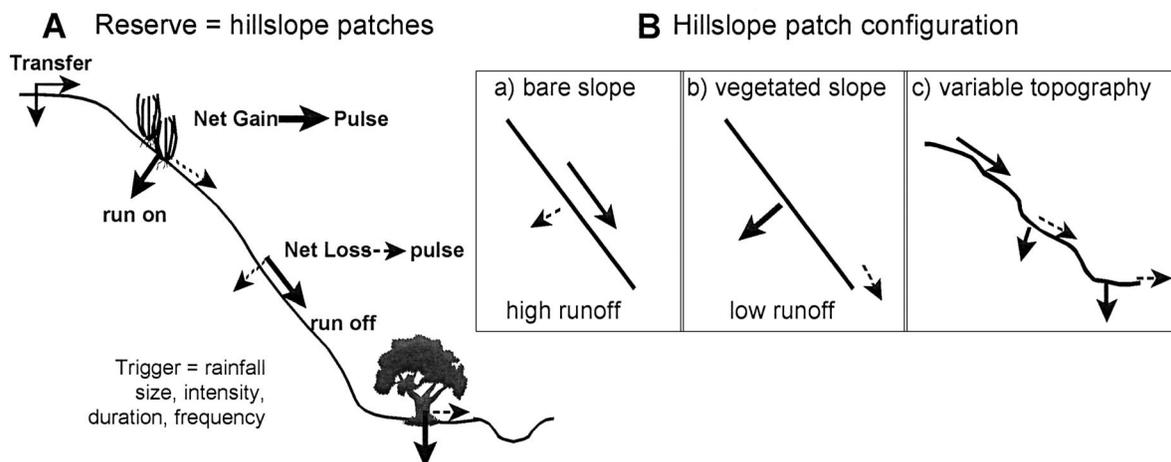


FIG. 3. (A) Stylized depiction of a desert hillslope including vegetated and non-vegetated patches arrayed along a topographical gradient from ridge top to valley bottom. Vegetated patches and topographic depressions have greater capacity to absorb rainfall, leading to greater pulses of microbial activity and less runoff when compared to plant interspaces. (B) Hypothesized effect of hillslope patch configuration on hydrologic and material retention. (a) Bare slopes have little capacity to absorb water and nutrients in comparison with (b) vegetated hillslopes, and those with (c) variable topography, including topographic flats or depressions. Since topographic depressions and vegetated areas increase retention, hillslope patch configuration may influence overall retention. As runoff volume and material redistribution increase (with increasing storm intensity), the effects of patch configuration on hillslope retention may become more pronounced.

concentrations from vegetated patches can also be high. In a hot desert, Schlesinger et al. (1999) reported runoff concentrations of total dissolved N from shrubs and intershrub plots as 1.44 and 0.55 mg N/L respectively, and estimated runoff losses from shrublands at 0.43 kg N·ha⁻¹·yr⁻¹ and grassland loss at 0.25 kg N·ha⁻¹·yr⁻¹. In a cool desert, Barger (2003) estimated N losses from BSC-covered interspaces to range from 0.15–1.5 kg·ha⁻¹·yr⁻¹, depending on BSC type. Nutrient losses from a given patch can serve as a resource subsidy for receiving patches or be lost from the system to downslope intermittent washes. These transfers result in nutrient redistribution within a catchment since losses decrease dramatically with increasing scale (Wilcox et al. 2003). As with BSC cover at the plant interspace scale, plant patches at the hillslope scale increase surface roughness and thus reduce the velocity of overland flow, increasing hydrologic and nutrient retention (Tongway and Ludwig 1997). Retention is concentrated in “runon” patches, generally plant bases and topographic depressions (Fig. 3).

There are other avenues of water and nutrient loss. Evaporation is significant in deserts and is affected by BSC and plant cover and composition. Evaporation is lower under lichen BSCs compared to bare soil or cyanobacterial BSCs (George et al. 2003). It is likely lower when interspaces are shaded by annual plants in wet years compared to dry years with no annual plants, although we could find no data on this. Puigdefabregas and Sanchez (1996) found plant patches dry more slowly during cold seasons than bare areas; however, during times of higher evapotranspiration, vegetated patches dry at comparable rates. Therefore, BSCs, vegetation,

evapotranspiration rates, and storm size and intensity influence which hillslope patches receive water and how long these patches remain wet or “active.” Downward leaching of C and N is thought to be very low in deserts (Seyfried et al. 2005), but may be substantial in coarse-textured soils, especially after low-intensity synoptic storms accompanied by high infiltration rates. Indeed, NO₃⁻, the most mobile N species, has been found concentrated to thousands of kg/ha at several meters depth in Southwestern deserts, indicating that leaching losses, and subsequent accumulation in the vadose zone, are a heretofore unaccounted yet substantial N output from surface ecosystems (Walvoord et al. 2003). Whereas overland flow, evapotranspiration, and leaching all result in water and nutrient loss from hillslope patches, they have very different consequences for microbial activity.

Pulse: carbon and nitrogen dynamics

Microbial activity only occurs when soils are wet. Therefore, the hillslope patch structure interacts with incoming rainfall to create a mosaic of microbial activity that varies with patch type. Timing of rainfall is important for microbes. Respiration begins immediately upon wetting, whereas photosynthesis requires light and optimal temperatures (Lange 2003). Thus, precipitation that occurs at night, in small events, and/or when soil temperatures are too high for photosynthesis often result in carbon (C) deficits (Jeffries et al. 1993). As these conditions often occur during desert summers, most hours available for inputs occur when temperatures are moderate to low (although variability among years is large; Table 1). Photosynthetic products are

TABLE 1. Hours during which soils were wet (volumetric water content $\geq 1\%$) and available for carbon fixation (daylight hours) and nitrogen fixation (daylight hours plus four nighttime hours) in southeast Utah in 2001.

Variable	Air temperature category ($^{\circ}\text{C}$)				
	<4	4–8	9–17	18–23	24–28
Hours available for carbon fixation	119	130	100	55	50
Hours available for nitrogen fixation	165	156	118	78	50

Notes: Values in boldface indicate those seasons with the highest number of hours available for C and N fixation.

required for N fixation and UV-protective pigment production; thus, C deficits impact these processes. Estimated C inputs range from 0.4 to 2.3 $\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ for cyanobacterial BSCs and 12–37 $\text{g C}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ for lichen BSCs (Evans and Lange 2003). In cool deserts, N inputs range from 1 to 10 $\text{kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ for cyanobacterial and lichen BSCs, respectively, and again most inputs occur at moderate to low temperatures (Table 1; Belnap 2002). The number and proportion of daytime hours that soils are wet varies considerably within and across seasons: in SE Utah, during 1999–2001, total hours soils were wet ranged from 131 to 200 (38–92% in daytime) in spring, 19–260 (42–58% in daytime) in summer, 60–400 (43–64% daytime) in fall, and 176–327 (53–76% daytime) in winter. This contributes to variability in annual C and N inputs. Because cool desert soils have lichen BSCs and more moist hours, they receive more fixed C and N than hot deserts with cyanobacterial crusts and fewer hours of soil water. During wet years and in slightly more mesic systems, the time available for microbial activity is increased, depending on the interaction between activity type and rainfall timing.

Wetting of dry soils can kill one-third to one-half of the soil microbial biomass through osmolysis, as many organisms accumulate solutes during dry periods to increase desiccation tolerance (Kieft et al. 1987), which results in C and N release that stimulates a pulse of microbial activity (e.g., Marumoto et al. 1982). Rapid increases in microbial biomass (Kieft et al. 1987) and microbial processes (e.g., N mineralization, nitrification) have been observed upon soil wetting (Davidson et al. 1990, Fisher and Whitford 1995). Photo-degradation of soil surface organic matter, atmospheric deposition of nutrients, and microbial death also occur between storms and may increase resource availability, stimulating microbial activity, particularly in areas receiving greater rainfall (e.g., semiarid).

Microbial respiration rates are 2–15 times higher in surface (0–5 cm) than deeper soil layers (5–15 cm; Bolton et al. 1993), but subsurface soils are wet longer (Puigdefabregas and Sanchez 1996). Therefore, the depth of the moisture pulse can also be important in determining when and where maximal C and N losses occur. Potential C and N mineralization rates are gen-

erally higher in vegetated plots than interspace soil (Kieft et al. 1998, Burke et al. 1999). During summer, spatial variation in microbial processes at the hillslope and landscape scale is expected to be high, due to high evaporation rates and the variable influence of aspect, slope, vegetation, and the localized nature of short, high-intensity rains. Because soil water is variable, both gaining (positive C and N balance) and losing (negative C and N balance) patches are expected during hot summer months, with less variability expected in winter. As precipitation increases from dry to wet years or arid to semiarid systems, pulses of microbial activity associated with rainfall may shift from water to resource limitation. While increased water availability may extend the period of activity during periods of high rainfall, rapid utilization of available C and N may lead to substrate limitation, causing rates of N loss to decline over time. Thus, while the relative activity level of a given process may increase between triggers, the overall size of the activity pulse may be dampened with increasing precipitation.

Losses of C and N also vary according to season, patch type, and desert type. In all deserts, N loss rates peak in the hot summer months. However, total losses during the three dry and hot summer months can be similar to losses during the wetter nine-month fall–spring season. Soils are warmer in hot deserts and the presence of N-fixing plants results in higher respiration and gaseous N loss rates than in cool deserts. In addition, vegetated and lichen BSC patches have higher rates of denitrification and respiration than bare or cyanobacterial BSC-covered interspaces (Virginia et al. 1982, Bolton et al. 1993, Lange 2003). Estimates of annual N losses (NH_3 , N_2O , N_2 , NO) from interspaces in cool deserts range from 0.56 to 1.60 $\text{kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ for cyanobacterial BSCs to 0.29–0.86 $\text{kg}\cdot\text{ha}^{-1}\cdot\text{yr}^{-1}$ for lichen BSCs (Barger 2003). N_2O loss rates for hot deserts are higher at 0.75 $\text{kg}/\text{ha}/\text{yr}$ (Guilbault and Matthias 1998). Due to the interaction of rainfall timing and air temperatures, cool, winter-rainfall-dominated deserts also show less overlap between the timing of maximal N inputs (fall, winter, spring) and losses (summer) than in summer-rainfall-dominated deserts, where maximum inputs and losses may coincide in time and space (summer). Disturbance is also important, as it is followed by increased loss and decreased input of C and N.

Feedbacks between transfer, reserve, and pulses

Many feedbacks influence the effect of precipitation events in deserts from the interspace to hillslope scale (Fig. 4). Water availability stimulates C and N fixation that is used to create more BSC and plant biomass. Increased biomass increases soil aggregates, soil surface roughness, and soil stability, all of which increase retention of water and organic matter (Tongway and Ludwig 1997). This retention results in more microbial activity and thus C and N fixation which then results in a further increase in microbial and plant biomass.

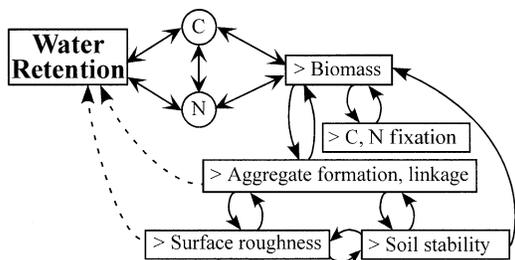


FIG. 4. Many feedbacks that occur in deserts influence the effect of moisture pulses on multiple scales, including those of the plant interspace patch, plant patch, and hillslope patch. The solid lines represent linkages that have been explicitly studied; the dotted arrows represent connections that require further study.

Because patches vary in their ability to intercept and retain water and provide nutrients, the strength of the feedback arrows will vary among patches. Spatial configuration and species composition (Huxman et al. 2005) of patches will also influence water and nutrient retention on the hillslope as a whole (Puigdefabregas et al. 1999), particularly as storm size and intensity increase (Fig. 3). Hillslopes end in valley bottoms or topographic depressions, which comprise riparian areas that line the banks of streams. Water and nutrients exported from hillslopes enter the stream network, beginning with small rills and rivulets which flow into progressively larger stream channels. Whereas we distinguish these small channels from the hillslope, the two are interwoven and each channel receives material from a sequence of hillslope patches.

STREAM NETWORK: INTERMITTENT TO PERENNIAL STREAMS

Reserves: riparian zones, channel sediments, and stream algae

Both longitudinal gradients (i.e., headwater to mouth) and hierarchical patch structure exist within stream networks that dissect arid landscapes. Overland flow from hillslopes quickly collects into rills that feed

ephemeral channels, thence to seasonally intermittent and, finally, perennial streams. Several characteristics of stream networks change predictably along this gradient (e.g., geomorphic variables described many years ago by Leopold et al. [1964]), with a threshold at the transition from ephemeral to perennial flow. Patch structure (reserves) of the stream–riparian corridor, which itself varies along the gradient, includes a riparian zone, channel sediments (sometimes called the active channel or parafluvial zone), and the wetted stream (Fisher et al. 1998; Fig. 5). Within each of these broad categories, additional patches form reserves (e.g., vegetation, groundwater and micro- or macroalgae), but we here focus on exemplary components rather than an exhaustive treatment.

For the water-limited elements of riparian zones, such as understory vegetation that does not access groundwater, precipitation likely triggers responses of soil microorganisms and pulses of microbial activity that are similar to those discussed for the hillslope. But the trigger-transfer-reserve-pulse model also operates quite differently in these catchment lowlands. Rain falling directly on stream channels and riparian zones will rarely initiate TTRP sequences; rather, pulsed responses are reliant upon connection with upflow events, either from the adjacent hillslope or upstream channel network with greater contributing upland areas capable of generating pulses in stream flow. In some cases, such as in large, perennial streams, the original source of the water (and nutrients) transferred to a reserve such as the riparian zone is located kilometers away. Unlike plant or interspace and hillslope scales, the rainfall trigger initiates the TTRP chain of events but also can represent an important ecosystem disturbance that initiates succession (Fisher et al. 1982, Grimm and Fisher 1989).

While it is tempting to compare the structure of the upland (plant island and interspace reserves) with that of the stream–riparian corridor (with riparian zones or the stream serving as the plant-island “analogue” and channel sediments as the interspace “analogue”), this

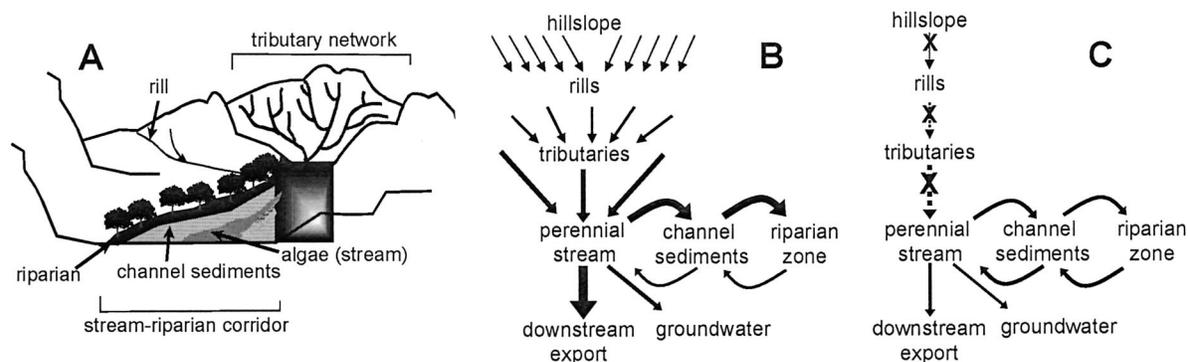


FIG. 5. (A) Stylized depiction of a desert watershed, showing a single, first-order rill, a network of ephemeral–intermittent tributaries of increasing order, and a close-up of the three components of a perennial stream–riparian corridor discussed as “reserves” in this paper. Panels (B) and (C) show different scenarios for hydrologic retention.

sort of contrast has limited utility. Hydrologic connectivity between the patches varies. Flash floods may represent an episodic connection between patches, triggering pulses of microbial activity in streams, much in the same way that small storms trigger pulses of activity on hillslopes. However, patches are not always linked exclusively during a triggering event; rather, connectivity may be continuous (e.g., under baseflow conditions).

Transfer: horizontal and vertical movement of water and nutrients

Gains.—Floods in arid regions often carry high concentrations of C and N (Grimm and Fisher 1992). For floods to represent a nutrient gain for the stream-riparian ecosystem, hydrologic retention must occur; otherwise all nutrients are quickly exported in surface flow. Hydrologic retention occurs in bank (riparian) sediments and in channel sediments that were unsaturated before the event (Fig. 5). Sediments to varying depths can act like a “sponge” to absorb and rapidly transmit floodwaters, even in smaller, ephemeral streams. For example, Martí et al. (2000) showed an almost instantaneous rise in water table elevation of riparian groundwater in response to summer flash floods in Sycamore Creek, Arizona. Hydrologic residence time in the stream, on the other hand, is exceptionally short, and during floods, the potential for biologically mediated pulses is very small. Thus residence time, and hence any gain of nutrients by the stream-riparian subsystems, is increased by transfer of water and nutrients into subsurface storage zones.

Losses.—Very large losses of nutrient reserves are incurred in the stream during floods, as most events with a discharge $>2 \text{ m}^3/\text{s}$ are capable of dislodging and/or scouring algae from the stream bottom (Grimm and Fisher 1989). In very large events, entire reserves are lost (riparian vegetation—even whole trees—can be exported, and channel sediments deeply scoured). Smaller events may simply redistribute materials and are less likely to have an impact on riparian zones (Fisher et al. 1998). Redistribution can occur within or among the three major reserves (riparian, channel sediments, stream). Sediment and dislodged algae can be deposited in the active channel or, in overbank floods, in the riparian zone, rather than being exported downstream.

Although we can think of rainstorms that are sufficient to produce flash floods in perennial streams in the context of the TTRP model, floods do not merely result in gain or loss; they also represent succession-initiating disturbances to the stream-riparian ecosystem. Subsystems of the stream-riparian corridor vary in their resistance and resilience to flood disturbance, so that succession occurs on a similarly wide range of time scales (Fisher et al. 1998). Stream algae come and go many times over the course of an average year, channel sediments and associated vegetation are resistant to

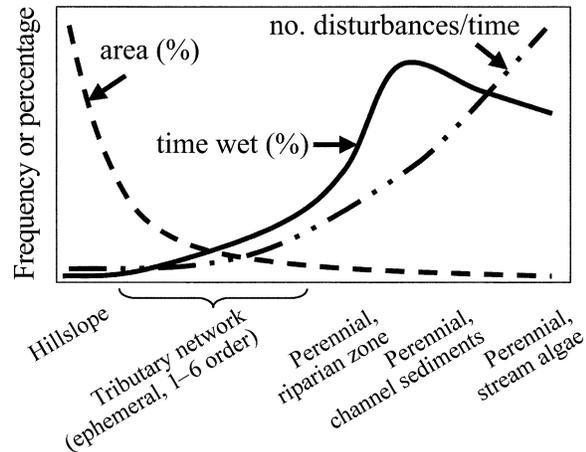


FIG. 6. Hypothesized longitudinal changes in spatial extent (percentage of area) of landscape components, temporal duration (percentage of time wet) of moist conditions, and disturbance frequency (no. events/time), in patches (reserves) from hillslope to perennial stream-riparian ecosystems. Patches are arrayed along a theoretical flow path.

smaller events but can be scoured and redeposited by floods of $\sim 5\text{--}10$ yr recurrence, and riparian forests may persist for decades or more. Whatever the scale, however, the “resetting” effect of floods is such that these systems are frequently in successional stages, and thus more likely to retain nutrients to support positive net biomass accrual (e.g., Grimm and Fisher 1986, Vitousek et al. 1998).

Transfers that continue between floods

Because remote triggers (both in space and time) that produce episodic events can result in continued flow even in the absence of further events, the delivery of materials to riparian, channel sediments, and stream algae continues long after the trigger has since dissipated. For example, nutrients that are delivered to riparian groundwater during the event may slowly drain out into the stream over a protracted period of days or even weeks (i.e., bank drainage). Higher-elevation rains that produce floods in low-order streams but not larger streams may trigger the transfer of floodwaters to alluvial groundwater, which reemerges much later and farther downstream at perennial “springs” in the mainstem (e.g., Dent et al. 2001). Thus, we can envision overlapping gradients of disturbance frequency and the percentage of time that a given point along the stream network (longitudinal) or across the stream laterally (from riparian zone to stream algae) is inundated (Fig. 6).

Pulse: carbon and nitrogen dynamics

Transfer of the high nutrient and C loads of floodwaters to riparian zones can support a flush of plant uptake (Schade et al. 2002) and microbial processing. Here, in contrast to the hillslope where the addition of

water triggers the pulse, it is high nutrient concentrations and changed nutrient form (e.g., nitrate or ammonium) that likely leads to increased process rates. Flood inputs of NO_3^- may spark a rapid denitrification response, as the process is often limited by NO_3^- availability in hypoxic riparian groundwater (Holmes et al. 1996). Rising water tables (a vertical transfer) inundate previously unsaturated soils and are more analogous to the pulses described for hillslope soils (e.g., Baker et al. 2000), although time to drying is surely longer in the riparian case.

In the stream, the transferred nutrients are less likely to produce a pulse of microbial or plant activity, because biota have been exported from the system by scouring floods. However, high nutrient concentrations can persist after flood recession (Fisher et al. 1982), and provide substrate for regrowing microbial and algal populations (e.g., Peterson et al. 1994). Previously dry channel sediments may exhibit pulsed activity due to solubilization of accumulated materials or reactivation of microbes, but the time course of activity following inundation is longer than in uplands.

In general, the stream and riparian patches of larger, perennial streams may exhibit fewer pulses of enhanced microbial activity than do plant and interspace patches, but some rapid and transient responses do occur (e.g., Groffman and Crosse 1999). Other processes may exhibit a step change and slow deterioration (owing to very slow drying or return to pre-event conditions), and others primarily reflect floods as succession-initiating events. In the framework of the TTRP model, reserves are reduced and losses dominate, until reserves begin to reestablish during succession.

For whole landscapes, event duration and spatial extent of a patch together may provide an index of the importance of any given landscape component to a landscape function like trace gas flux or N fixation (Fig. 6). However, we also must consider floods that “reset” patches within streams, reducing the percentage of time that perennially wet patches are active (i.e., no biota = no processes). These ideas are reflected as changes in the predicted importance of areal contribution, duration of favorable moisture conditions, and disturbance frequency, along presumptive flow paths from uplands to large stream-riparian ecosystems in the desert.

MICROBIAL-HYDROLOGICAL LINKAGES FROM PLANT INTERSPACES TO STREAMS

As illustrated in the previous sections, significant precipitation events can trigger an interplay of microbial and hydrological processes. Water, soil, nutrients, and organic materials, including soil biota, are transferred across the landscape. These spatial transfers vary in scale from plant interspaces to plants, to entire hillslopes, to drainages and streams that drain many hillslopes. The magnitude and duration of biological activity pulses are variable in both space and time. The

strength of linkages between transfers and pulses across all these spatial and temporal scales are critical to maintaining the functioning of arid and semiarid landscapes. To illustrate this, we follow the fate of some organic matter through the landscape.

As described in the uplands section, rain falling on a biological soil crust triggers a pulse of C and N fixation, which is then converted to greater crust biomass. This new organic matter also contributes to new or stronger soil aggregates, and thus greater soil stability; increased C to microbial populations and thus greater activity rates; greater soil surface roughness and thus greater water infiltration; and more crust biomass to fix more C and N fixation during the next rainfall event. At this fine scale, these positive feedback loops or linkages are clearly important to maintaining highly functional and healthy plants and interspace soil crusts.

However, disturbances, such as hoof action by livestock, can fracture crusts, so that fragments are dislodged and transferred downslope with runoff. Runoff (and, in this example, the fragment of biological crust) may be captured by a patch of vegetation on the hillslope. This gain of water and organic matter triggers a pulse of microbial growth and activity (e.g., nitrification and mineralization) and vegetative growth on this hillslope patch. With these additional resources, microbial activity is stimulated, including additional C and N fixation, under the plant canopy. This contributes to greater plant biomass and strengthens the vegetative structure that allows capture and retention of runoff in the next rainstorm. These positive feedbacks maintain functional and healthy landscapes at the hillslope scale. There is also a negative feedback that occurs as increased plant biomass transpires more water, decreasing soil moisture and microbial activity time.

When high-intensity summer storms occur such that rainfall rates exceed the infiltration capacity of the interspace or plant-island patch, overland flow results. These strong flows will redistribute materials among hillslope patches, or carry our fragment of soil crust into riparian patches along a drainage line. As described in the stream network section, the delivery of such organic materials, nutrients, and water to riparian zones produces a pulse of microbial or plant activity in this zone. As before, increased C and N inputs strengthen the riparian zone by enhancing capture and retention of such deliveries in the next overland flow event. In fact, the riparian zone and its associated channel can act as a “sponge” for water, mineral nutrients and organic matter carried in such flows. However, our fragment of soil crust can be swept into the stream channel and exported out of the system during large, scouring floods.

Following the hypothetical fate of a soil crust fragment illustrates how hydrological processes and microbial activities are linked in arid and semiarid landscapes. When these landscapes are highly functional or healthy, feedback linkages are strong, maintaining or

even improving the functionality of the landscape. Losses of organic matter, nutrients, soil, and water are natural processes, but we become concerned when such erosion losses exceed the natural range of variability, as the landscape system is no longer “conserving,” but “leaky,” and losses exceed gains in the TTRP framework (Ludwig and Tongway 1997). In these ways, such linkages define the structure and function of arid ecosystems. Consequently, conservation in desert areas will require understanding the nature and vulnerability to disturbance of these linkages.

FUTURE DIRECTIONS

Truly understanding how the effects of a given precipitation event reverberate through desert landscapes is a difficult and complex problem. Although we have presented an outline of the process that occurs, our description lacks many details. For example, we have much more information on soil processes in cool deserts than in hot deserts. In contrast, we have much more information about stream processes in hot deserts than is available for cool deserts. This calls for a more integrated approach to research efforts at a given site, and study of a more diverse set of sites.

Desert landscapes provide particularly useful testbeds for understanding hydrologic and biogeochemical interactions between terrestrial and aquatic ecosystems because, as we have argued here, the connection between upland and lowland patches is episodic and mostly aboveground. However, human-induced climate change may alter regional hydrology, for example, through increased precipitation or intensification of the hydrologic cycle. Thus, a more complete understanding of the processes we have discussed along gradients of precipitation, or between years differing in frequency and timing of extreme events, will greatly add to this nascent understanding. We contend that the TTRP framework, as modified by considering the spatial and temporal extent and duration of water availability, provides an appropriate conceptual model for both terrestrial and aquatic components of desert landscapes under current and uncertain future conditions.

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